Life History of *Trupanea conjuncta* (Adams) on *Trixus californica* Kellogg in Southern California (Diptera: Tephritidae)

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Abstract.—*Trupanea conjuncta* is monophagous on the desert shrub, *Trixus californica* (Asteraceae), in southern California. Each female oviposits an average of five eggs in a single cluster in a single immature flower head each day. The larvae feed and develop gregariously and pupariate clustered in central cavities in flower heads. This tephritid may be either univoltine or bivoltine; consequently, the adults may live as long as a year. Unique among *Trupanea* spp. and other flower head-infesting Tephritidae as known to date, this species is a facultative gall former. If flower heads are absent or rare from a lack of local rainfall, gravid females may oviposit in apical buds and the larvae develop to maturity gregariously in the galls so induced. Thus, another reason for gall formation by insects has been discovered, i.e., as an alternative mode of reproduction and development by a flower head-infesting species. Egg resorption also may have evolved as a mechanism for extending the ovipositional period and host-searching capacity of this fly. *Eurytoma vernonia* Bugbee (Eurytomidae) and *Pteromalus purpurieventrus* (Ashmead) (Pteromalidae) are reported as probable, primary, hymenopterous parasites of the larvae and pupae.

Little heretofore was known about *Trupanea conjuncta* (Adams), except taxonomically. I recently studied this distinctive tephritid in conjunction with a faunistic survey of the desert shrub, *Trixus californica* Kellogg (Asteraceae), in southern California (Goeden and Ricker, unpublished data).

Taxonomy.—First described as *Urellia conjuncta* by Adams (1904). *T. conjuncta* additionally was described and illustrated in part by Malloch (1942) (as a *Trypanea*), Foote (1960a) and Foote and Blanc (1963) (as a *Trupanea*).

Distribution and hosts.—Before publication of the initial host-plant rearing record for this tephritid from flower heads of *T. californica* (Goeden 1983), *T. conjuncta* was described as "rarely collected" from only a few locations in Arizona and California (Foote 1960, Foote and Blanc 1963). This fly presumably also ranges into Mexico like its host-plant (Shreve and Wiggens 1964), the sole representative of the genus *Trixis* (Tribe Mutisieae) in the Sonoran Desert flora of Arizona (Kearney and Pebbles 1964) and California (Munz and Keck 1959, Munz 1974). Additional species of *Trixis* in the Sonoran Desert in Mexico (Shreve and Wiggens 1964) represent potential hosts.

I have reared *T. conjuncta* only from flower heads (and terminal-bud galls, as described below) of *T. californica,* among 77 genera and 182 species of California Asteraceae sampled to date. Thus, *T. conjuncta* apparently is monophagous in California (Goeden 1985). My rearing records from *T. californica* flower heads

collected on the dates indicated include the following: Imperial County: Indian Well, one male and two females, 12.iii.86; Mountain Spring, two males, 20.iii.86; Riverside County: Desert Center, 108 males and 108 females, 14.iii.84; Graham Pass, 47 males and 41 females, 21.iii.84; San Bernardino County: Coxcomb Mountains, 40 males and 39 females, 20.iii.84; Sheephole Mountains, 14 males and 19 females, 14.iii.84; San Diego County: Coyote Canyon, one male and one female, 29.ii.84; Yaqui Pass, three males and three females, 11.i.84. Goeden (1983) recorded *T. conjuncta* from Chino Canyon, ca. 1 km NW of Palm Springs, Riverside County, where most field observations reported herein were made and flower head samples collected for dissection during 1983–86.

Biology

Egg.—Newly laid eggs (Fig. 1a) are smooth, shiny, white, and elongate ellipsoidal, with a reduced, button-like, anterior pedicel, like those of *T. bisetosa* (Coquillett) (Cavender and Goeden 1982). The posterior end narrows to a smoothly rounded point and usually is covered and partly obscured by a whitish secretion that glues together this end of several eggs deposited in a packet (Fig. 1a). Thirty-four field-collected eggs averaged 0.77 ± 0.008 (± SE) mm in length and 0.18 ± 0.003 mm in greatest width. The pedicels averaged 0.03 mm in length and width. The eggs of *T. conjuncta* are slightly longer and narrower, the pedicels slightly shorter than those of *T. bisetosa* (Cavender and Goeden 1982).

Unlike the eggs of *T. nigricornis* (Coquillett) and *T. bisetosa,* which are deposited singly (unpublished data, and Cavender and Goeden 1982, respectively), the eggs of *T. conjuncta* usually are deposited in groups glued together posteriorly and along part of their lengths. The egg clusters were easily lifted as units from the tips of the floral tubes among the pappus hairs where the eggs usually are oviposited with their long axes perpendicular to the receptacle surface. The "glue" loses its stickiness with time. One or more outer eggs in a packet may also be glued to the inner curve of a receptacle bract or to the adaxial surface of an inner phyllary. As these bracts subsequently elongate, the attached cluster of egg chorions (by then usually empty) is lifted upwards and away from the receptacle. All eggs in a packet are deposited together by one female at a single insertion of her ovipositor, which usually penetrated one or more of the leaves surrounding the young flower head and one or two of the enveloping, alternately arranged phyllaries. The path of the ovipositor was marked by circular punctures ca. 0.15 mm in diameter ringed by brown necrotic tissue. Some oviposition occurred through the opening at the apex of a young flower head where the tips of the phyllaries met. Only five (8%) of 60 infested heads examined contained two egg packets (Fig. 1a), apparently laid by different females or at least at different times, judging from the numbers and patterns of the egg punctures as well as the different stages of development of the eggs in each pair of egg clusters. The number of eggs in 65 clusters from field-collected heads averaged 4.5 ± 0.1 (range: 3 to 7). The most eggs found in an infested head was 12. Females preferred early-stage flower heads only 3 to 5 mm long for oviposition; this stage lasted only two or three days in the field. Oviposition did not always follow probing, as evidenced by punctured phyllaries of uninfested heads. Caged females were not deterred from laying a superabundance of eggs in single buds. At least one egg mass was observed that had been deposited atop another mass in nature. This behavior
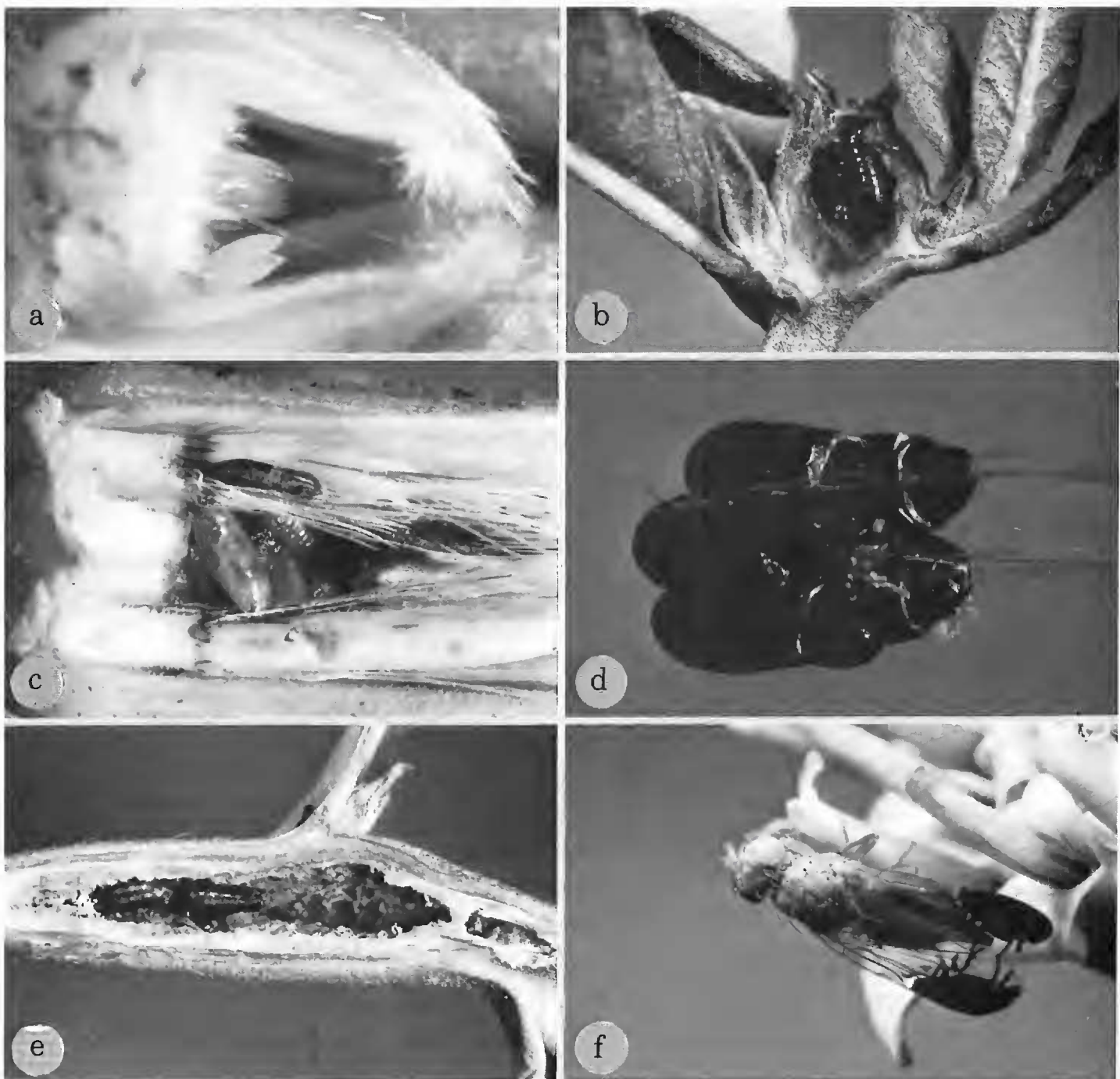
Figure 1. Life stages of *Trupanea conjuncta.* (a) Two egg clusters in young flower head, 16x. (b) Subspheroidal gall containing puparia, 4.3x. (c) Third instars feeding gregariously in flower head, 6.4x. (d) Cluster of empty puparia from flower head, 9x. (e) Ellipsoidal gall containing puparia, 4.3x. (f) Adult female at rest on flower head of *Trixus californica,* 6.6x.

suggested that the short duration of the attractive stage of development of the young heads, not the use of a marking pheromone as occurs with certain frugivorous Tephritidae (Prokopy 1972), limits egg deposition in heads. Females of *Tephritis dilacerata* Loew (Berube 1978) and *Trupanea bisetosa* (Cavender and Goeden 1972) also apparently did not recognize or avoid immature flower heads that already contained eggs.

The clustering of eggs by *T. conjuncta* apparently is an adaptation for a unique feature of its life history, i.e., the capacity for facultative gall formation, a feature never before reported for any flower head-infesting tephritid. No other species of *Trupanea* is known to form galls; however, this behavior provides additional ecological evidence linking this genus to the closely related genus *Tephritis,* several

species of which are gallicolous (Quisenberry 1951, Foote 1959, 1960a, 1960b). This behavior may have gone undetected if an associate and I had not concurrently surveyed the insect fauna of *T. californica* at various desert locations (Goeden and Ricker, unpublished data) while I studied the life history of this fly. When surveying plants in Grapevine Canyon, NE San Diego County, in early February, 1984, I found terminal bud galls on branches of plants that had not yet experienced rainfall that winter, and probably not since the previous winter. Field and subsequent laboratory examinations showed that these galls contained tephritid puparia from which *T. conjuncta* adults subsequently were reared (Fig. 1b). If gravid mature females cannot find young flower heads generated on host plants in response to winter or late summer rainfall, they apparently will oviposit small groups of eggs in the apical buds. Facultative gall formation sems to be a mechanism that this flower head-infesting tephritid has evolved to insure its reproduction for at least another generation under conditions of inadequate rainfall or flower head availability. No galls were formed on *Trixis* which flowered in February through April, 1984, in response to rainfall received at the Chino Canyon site in January and the preceding December. Thus, gall formation was a localized, facultative activity. However, several old, woody galls were observed on the stems at Chino Canyon, which indicated that gall formation also had occurred there about two growth periods beforehand. No other species of insect produces galls on stems of *T. californica* in southern California (Goeden and Ricker, unpublished data).

Twenty-four eggs hatched after six to eight days' incubation at $27 \pm 2°C$ and 100% relative humidity in the laboratory. When denied their usual ovipositional sites during solitary greenhouse cagings on non-flowering branches of *Trixis,* individual, field-collected, sexually mature and mated females stored their eggs internally for as long as a week. This denial of ovipositional sites occasionally resulted in the insertion of some eggs in apical buds, the prerequisite for gall formation in nature. If immature flower heads were resupplied to these caged gravid females after several days, eggs were laid within the heads in large clutches, e.g., 18, 22, and 30 eggs, and various stages of embryony, including those that hatched only one or two days after deposition. Thus, embryony continued within the oviduct, as apparently did egg resorption, as indicated by the oviposition of empty egg chorions together with partly reabsorbed, flaccid eggs and viable, turgid eggs. Whether egg resorption occurs in gravid females of *T. conjuncta* in nature is unknown. Conserving egg metabolites in this manner would be another mechanism for extending the reproductive life and host-searching capacity of this desert-inhabiting tephritid, which is solely dependent for its reproduction on a localized, fairly uncommon, single species of host plant growing suboptimally at the northernmost extension of its range. In January, 1985, a severe winter frost killed the top growth and delayed or prevented flowering of many *T. californica* in southern California, an event of the type which egg resorption and the resultant extended female ovipositional period may have evolved to counter.

In flower heads, the embryo rotated 180° just before hatching, so that the mouthparts of the first instar usually were immediately in contact with a floral tube upon leaving the egg through a posterior-longitudinal slit in the chorion. The duration between eclosion of the first and last individuals from a single egg clutch was ca. one day.

Larva.—The larvae of *T. conjuncta* usually fed gregariously. I observed only one instance in flower heads in which the newly hatched larvae from a single cluster had

split into two feeding groups that attacked separate florets. All larvae newly hatched from an egg cluster usually entered the elongating floral tube of a single floret together and tunneled basipetally into the immature achene. After consuming the contents of this first floret, the larvae together transferred to an adjacent floret which they entered through the base of its floral tube. Feeding within a series of florets continued in this manner through the second stadium; however, most feeding and larval growth occurred during the third stadium. The third instars fed in a central ellipsoidal cavity (6 to 9 mm long) ca. 3 mm wide, formed among the stumps of achenes, the scored receptacle, and the distal remnants of the pappus hairs of the central florets excised 2 to 3 mm from their tips, all surrounded by a ring of scored or undamaged florets (Fig. 1c). As many as 12 third instars fed in a compact mass within a moist, central cavity, the walls of which were covered with yellowish, liquid feces (Fig. 1c). When fully grown, the larvae pointed their mouthparts acropetally, ceased movement, and pupariated in a compact cluster (Fig. 1d).

The galls of *T. conjuncta* are initiated when a female oviposits in a terminal bud. The round ovipositional scar was seen on the surface of some galls. Upon hatching, the larvae feed on the surrounding tissues and extend the gall cavity into the pith of the branch tip. If this feeding killed the apical meristem, the branch ceased to elongate and a subspheroidal gall resulted (Fig. 1b). If the apical meristems remained intact, the gall assumed a spindle shape as the branch continued apical growth (Fig. 1e). Twenty-one field-collected, current season's galls measured 9.7 ± 0.6 (range: 6 to 16) mm in length and 4.6 ± 0.1 (range: 3.6 to 5.5) mm in greatest width. The larvae fed on the parenchymatous pith tissue, expanding the gall cavity in length and width until, eventually, two to five shortened internodes were incorporated in the fully formed galls. The central cavities of 13 fully formed galls averaged 6.3 ± 0.4 (range: 3.3 to 9.0) mm in length and 2.6 ± 0.2 (range: 1.0 to 3.5) mm in width. The cavities were ellipsoidal (Fig. 1e) or subspheroidal (Fig. 1b), smooth-walled, and free of frass. none, several, or all of the axillary buds along the length of the gall, instead of or as well as the terminal bud, may break dormancy and grow into branches. The vascular cylinder is incorporated in the wall of the gall, which remains green and photosynthetic while the gall remains occupied. The fully grown larvae cut one or two short emergence tunnels, usually laterally in the distal half of the galls, through the 0.75–1.25 mm thick walls, leaving a thin flap of epidermis covering each future exit hole. The larvae usually pupariate with their head directed acropetally towards an exit tunnel. Some larvae pupariated in a partially overlapping linear row and formed only a single, common exit hole (Fig. 1e).

It is but one evolutionary step for a species to gall axillary buds in addition to terminal buds as occurs with other genera and species of Tephritidae, e.g., *Aciurina*, *Procecidochares*, and some *Tephritis* (Foote 1960b, Silverman and Goeden 1980, Steyskal 1984). Moreover, facultative gall formation, as expressed by *T. conjuncta*, indicates one means by which a flower head-infesting species of Tephritidae may have evolved sympatrically into a gallicolous species occupying a different niche on the same host plant, or vice versa. In a separate paper, I will describe an apparent example of facultative gall formation in the genus *Tephritis*. Whether oviposition of egg clusters and gregarious larval and pupal development are adaptations reflecting a gall-forming ancestry or facilitating reproduction in galls by a flower head-infesting

species, or are prerequisites thereof, I leave to evolutionary ecologists and systematists to interpret.

Pupa.—Pupation occurs in a puparium within the central cavity in a flower head or gall (Fig. 1e). The puparium (Fig. 1d) is black, ellipsoidal, smoothly rounded at both ends, but with a flattened, posterior, perispiracular plate, superficially smooth, but very finely punctate, and slightly flattened or concave ventrally. Twenty-one field-collected puparia measured 3.1 ± 0.1 (range: 2.3 to 3.8) mm in length by 1.3 ± 0.04 (range: 1.0 to 1.6) mm in greatest width. Adults emerged through an anterior, two- or three-part fracture of the puparium. A very thin, whitish, translucent pupal exuvium, left behind within the puparium, also helps to distinguish unparasitized individuals. Adults emerged by pushing through the loose plug of excised tips of pappus hairs of the central florets, or by breaking through the epidermal windows covering the exit holes of galls.

Adult.—The adult (Fig. 1f) of both sexes is readily distinguished from other species of *Trupanea* by the unbroken dark to light-brown area in the distal anterior quarter and proximal half of the wing (Foote 1960a, Foote and Blanc 1963). Newly emerged adults are sexually immature and apparently do not mate. Judging from the rearing records reported above and my recovery of 394 males and 315 females (1.25:1) from 22 flower head samples collected at Chino Canyon during 1983–85, the sex ratio of *T. conjuncta* appears to be slightly male biased ($X^2 = 8.79$, p < .005, 1 df). Males outnumbered females in 15 of the 22 samples, whereas females outnumbered males in only five samples. *T. conjuncta* males were not observed to emerge from flower heads before females, as Silverman and Goeden (1980) reported for *Procecidochares* sp. from bud galls on the desert ragweed, *Ambrosia dumosa* (Gray) Payne. The latter tephritid also showed a male-biased sex ratio.

The adults of *T. conjuncta* probably are long-lived. They apparently pass the summer at higher elevations, moving upward along streams and washes into the surrounding mountains as flowering ceases and their perennial hosts become dormant. A portion may reach mountain meadows by midsummer, as occurs with the more common, also monophagous, desert species, *Trupanea imperfecta* (Coquillett) (unpublished data). As fall and colder weather approaches, the adults migrate towards lower and warmer elevations, where they eventually rendezvous on their host plants. I have not observed mating, which may occur in the field at this time or earlier at higher elevations. if summer rainfall stimulates a second bloom in the fall, these flower heads are used as oviposition sites. If their host plants remain dormant for lack of rainfall, I suspect that rather than form galls at this time, the flies remain inactive through the fall and early winter, awaiting the more dependable occurrence of winter rainfall and the resulting main flowering period. Consequently, mating either occurs in the fall in response to unknown stimuli to host flowering, or if no rain falls, is delayed until winter, or recurs then. Both sexes were swept from actively growing hosts before bud formation and oviposition commenced.

Oviposition was observed only once in the field at 10:21 A.M. on February 17, 1984, and lasted only 35 seconds. Oviposition is not commonly observed with this tephritid because (1) the adults *per se* are uncommonly observed or swept (Foote and Blanc 1963), even in close proximity to or directly from their host plants (personal observation); (2) most of that portion of their adult lives that is spent on or near their hosts appears to involve resting motionless (characteristically with wings slightly

parted but mostly overlapped atop the abdominal dorsum [Fig. 1f]) while hidden and sheltered within the crowns (especially when it is windy, as so commonly is the case in the winter and early spring on the Colorado Desert); and (3) each female apparently oviposits on the average only once a day in a single flower head. The last-named behavior is extrapolated from the results of greenhouse cagings of field-collected, gravid females mentioned above. Five females individually caged between March 6 to April 25, 1986, for one to 11 days each on single, flower bud-bearing branches of potted plants laid a total 387 eggs over a total of 75 days of cagings for an average of 5.2 eggs laid per female per day. This daily oviposition rate approximated the mean number of 4.5 eggs per cluster found in field-collected heads as reported above. The most eggs laid by a single caged female were 137. She apparently died prematurely and produced fertile eggs up to her death. As she probably had oviposited before being collected, this number of eggs underestimated her fecundity.

Seasonal history.—Munz (1974) described the flowering period of *T. californica* as February to April in southern California. I have reared *T. conjuncta* from mature flower heads collected on May 13 and 25, June 7, and October 3, 1983, in addition to February to April, 1983, 1984, and 1985, at Chino Canyon. Thus, this tephritid and its host plant had two reproductive periods in 1983, but only one in 1984 and 1985.

On March 7, 1985, 50, 50, 30, and 50 flower heads on four plants, respectively, were tagged individually by slipping rubber bands attached to number tags over the heads in the early stage favored for oviposition by *T. conjuncta*. The development of each of these heads subsequently was followed and correlated with tephritid adult emergence. From oviposition in young heads to adult emergence from mature flower heads with faded yellow or white florets that contained fully formed achenes, the immature stages of *T. conjuncta* and flower head development lasted about five weeks under field conditions. As discussed above, the adults appear capable of living as long as 12 or 13 months under field conditions in southern California.

Mortality factors.—The larvae of an apparently undescribed microlepidopteran, *Homeosoma* sp. (Pyralidae), each destroyed the contents of several young flower heads during the course of their development, occasionally including heads infested by *T. conjuncta*. Jumping spiders (Araneida: Salticidae) and crab spiders (Araneida: Thomisidae) appeared to be the most common potential predators of adults observed on preblossom and flowering host plants. Two species of Hymenoptera, both reared from flower heads of *T. californica,* were probable parasites of immature *T. conjuncta* and two other synphagous species of Tephritidae, *Tomoplagia cressoni* Aczel and *Trupanea actinobola* (Loew) (unpublished data). They were *Eurytoma vernonia* Bugbee (Eurytomidae), probably a solitary, primary, larval or larval-pupal endoparasite, and *Pteromalus (Habrocytus) purpurieventrus* (Ashmead) (Pteromalidae), probably a solitary, primary, larval ectoparasite. *Eurytoma vernonia* also were reared from puparia in apical bud galls, so adoption of this facultative mode of reproduction by *T. conjuncta* does not confer "enemy-free space" (Zwölfer 1983, Price et al. 1986); however, this could provide a measure of relative protection from natural enemies. Both chalcidoids parasitize *Trupanea imperfecta* in flower heads of *Bebbia juncea* (Bentham) Greene, another shrubby, perennial, desert Asteraceae that often grows in association with *T. californica*. The life history of *T. imperfecta* will be described in a separate paper.

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